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Soil Spore Bank of Ferns in a Gallery Forest of the Ecological Station of Panga, Uberlândia, MG, Brazil

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ABSTRACT.—The soil spore bank of ferns is a biotic component of plant communities, important for regeneration processes, population dynamics, and conservation programs. Each year it is enriched when new units are incorporated, and impoverished when they are lost by predation, loss of viability, or by germination. Soil was collected in three microhabitats of the gallery forest of the Panga Stream, at four depths, in the wet and the dry seasons. In general, independent of the season, 'dike' samples presented lower numbers of viable spores when compared to samples from the 'middle' and 'edge' of the forest. The number of viable spores and the number of fern species represented decreased with depth. At the end of the dry season, the number of viable spores decreased only in the first centimeters of the soil. Viable spores of thirteen terrestrial species were registered in the soil of this gallery forest. The presence of viable spores in the soil after six months drought and in deeper soil layers shows the existence of a persistent soil spore bank in the gallery forest of the Panga Stream.

A diaspore bank is a biotic component of soil where dispersion units in quiescence or dormancy are found. This biological store can be enriched or impoverished each year, when new units are incorporated, or lost by predation, loss of viability, or germination. Therefore, the diaspore bank is a dynamic component that represents a continuous source of dispersion units important for regeneration processes and population dynamics of plant communities. It is this biological and genetic potential in the soil which permits the local survival of the species during unfavorable environmental conditions or disturbances.

Most of the information about diaspore banks is related to the soil seed banks of plant communities (Fenner, 1985, 1995; Leck *et al.*, 1989; Baskin and Baskin, 1998). There is little information on the diaspore banks of bryophytes (Carroll and Ashton, 1965; During and ter Horst, 1983; During *et al.*, 1987; Leck and Simpson, 1987) and fern spore banks (Carroll and Ashton, 1965; Wee, 1974; Strickler and Edgerton, 1976; During *et al.*, 1987; Leck and Simpson, 1987; Hamilton, 1988; Lindsay and Dyer, 1990; Milberg, 1991; Dyer and Lindsay, 1992; Milberg and Anderson, 1994; Penrod and McCormick, 1996; Raffaele, 1996; Schneller and Holderegger, 1996). Sometimes the concept of banks must be amplified to include cases like the belowground structure bank of *Botrychium*, which is formed by gemmae, gametophytes, sporelings, and spores (Johnson-Groh *et al.*, 2002). For Tropical America, where there are about 3000 fern species, there is little information regarding spore banks (Pérez-García *et al.*, 1982; Simabukuro *et al.*, 1998, 1999).

Viable fern spores are encountered in different kinds of soil under natural vegetation or agricultural crops, with or without sporophytes near the sample

site, and in barren soil (Strickler and Edgerton, 1976; During and ter Horst, 1983; Clymo and Duckett, 1986; Leck and Simpson, 1987; Milberg, 1991; Dyer, 1994). These data confirm that fern spore dispersion occurs over long distances as indicated by Conant (1978) and Page (1979), among other authors, and that viability is maintained under natural conditions and during cultivation of the soil at least for non-chlorophyllous spore species.

Soil spore banks of ferns are believed to play an important role in the reproductive success of many species, creating numerous opportunities for spore germination and gametophyte establishment after any form of soil disturbance (Lindsay *et al.*, 1992; Dyer, 1994). Moreover, a large spore bank means that many gametophytes, originating from many different sporophytes, could develop at the same time in a limited space after disturbance of the vegetation, increasing the chance for mating of different genotypes (Milberg, 1991). Asexual reproduction by gametophytic gemmae in *Trichomanes speciosum* Willd. appears to be the principal kind of dispersion of the species in recent times, and the genetic variability may be attributed to sexual reproduction and spore dispersal in historic times under more favourable climatic conditions (Rumsey *et al.*, 1999). For this type of endangered species, with sporophytes extremely rare and vulnerable in the actual European climatic conditions as indicated by the authors, the soil spore bank could participate in the restoration of species heterozygosity. Soil spore banks also play a relevant role in conservation programs (Dyer and Lindsay, 1996), permitting the propagation of rare or endangered species by means of small soil samples collected without environmental disturbances (Lindsay *et al.*, 1992; Dyer, 1994).

The purpose of this paper is to characterize the fern soil spore bank for three microhabitats included in the gallery forest of the Ecological Station of Panga, Uberlândia–MG, Brazil.

Materials and Methods

The Ecologial Station of Panga is situated in Uberlândia, State of Minas Gerais, Brazil (19°09′20″–19°11′10″ S, 48°23′20″–48°24′35″ W, ca. 800 m altitude). Until 1984 the area occupied by the Ecological Station of Panga was a farm with agriculture and cattle breeding as its principal activities. The owners preserved the gallery forest. In 1985 the Federal University of Uberlândia bought the area and the vegetation recovered naturally. Today it is considered a representative area of cerrado for Central Brazil. Its 409.5 ha are occupied by cerrado *sensu lato* (Schiavini and Araújo, 1989; Ratter, 1992). Gallery forest, a component of the mesophytic forests of the Ecological Station of Panga, is situated along Panga Stream. The approximately 1.0 hectare area, from which the soil samples were collected, is situated on the left bank of the stream, 900 meters from the main road (Fig. 1).

'Dike', 'middle' and 'edge' are three microhabitats described by Schiavini (1992, 1997) for this gallery forest. The 'dike' is a natural elevation that borders the stream and extends 10 m out from the stream bank. According to Schiavini

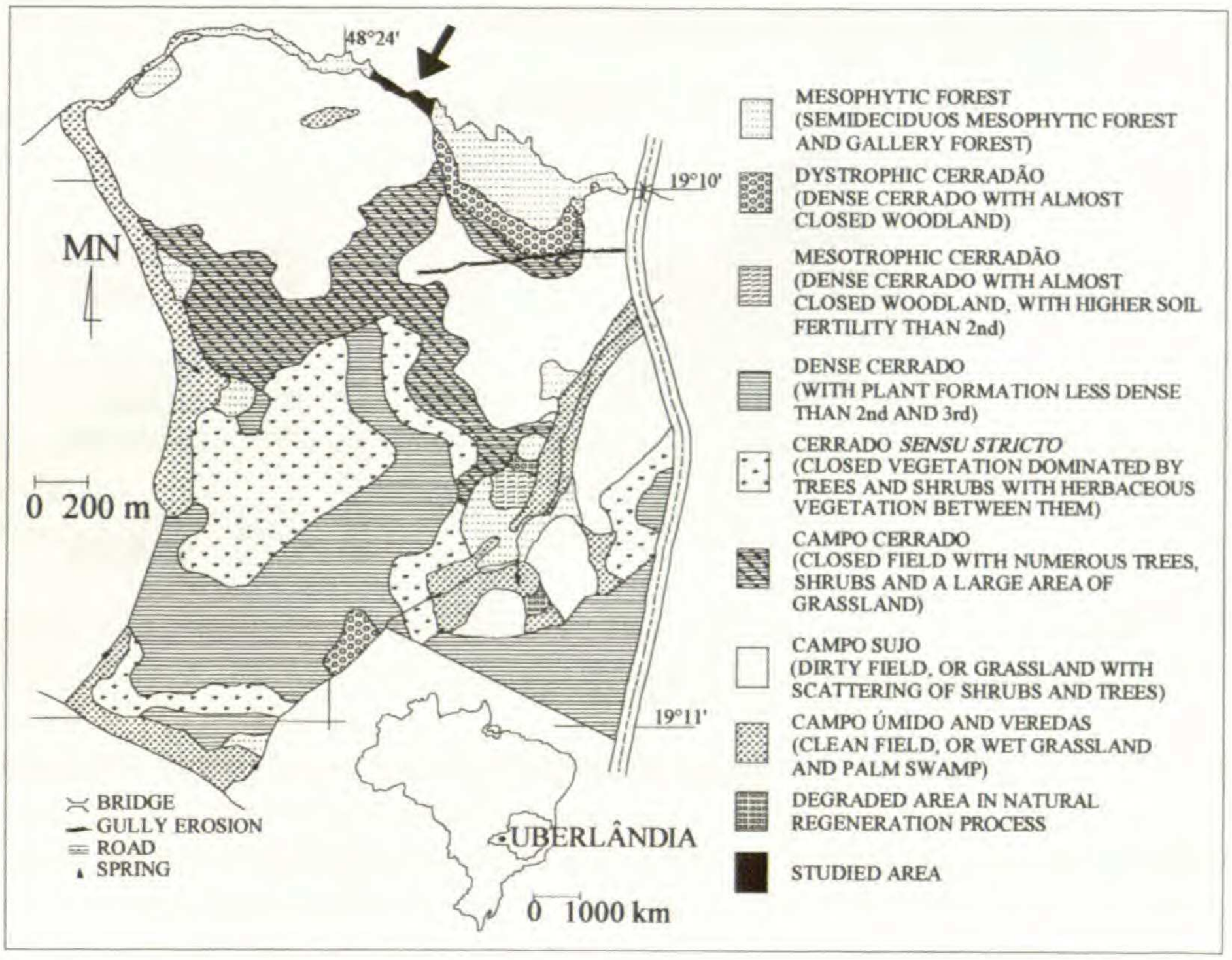

FIG. 1. Location and vegetation map of the Ecological Station of Panga (adapted from Schiavini, 1992).

(1992, 1997), fluvial sediments are deposited in this area, making the surface higher than 'middle'. Its soil consists of 85.2% sand, 5.5% silt, 9.3% clay, and 2.9% organic material, having good drainage. The 'middle' is a continuous depression adjacent to the 'dike', varying in width from zero to 40 m along of the stream. This microhabitat presents clay hydromorphic soil, consisting of 52.1% sand, 16.4% silt, 30.6% clay, and 9.2% organic material. It is flooded seasonally and saturated with water most of the year. The 'edge' of the forest is approximately 10 m wide. It has a Dark-Red Latosol (Oxisol) and a hydromorphic soil, depending on location and depth, with 75.6% sand, 9.3% silt, 15% clay, and 4.3% organic material. The water table in this microhabitat can vary in depth from just below the soil surface, for most of the year, to more than 0.5 m deep.

The region is included in Köppen's climatic system (1948) as Aw; that is, a tropical wet climate with dry winter. The wet season occurs during the summer, from October to March, and the dry season during the winter, from April to September (Fig. 2).

In February 1997, September 1997, and September 1998, soil was collected at four depths, in the three microhabitats of the gallery forest. In April 1998, soil was collected at two depths from the 'edge' microhabitat (Table 1). For each collection date, five holes of 40 cm depth and 900 cm^2 of opening (soil collection sites), approximately 10 m distant from each other were opened in each microhabitat. Each soil collection site was used only once. Soil of

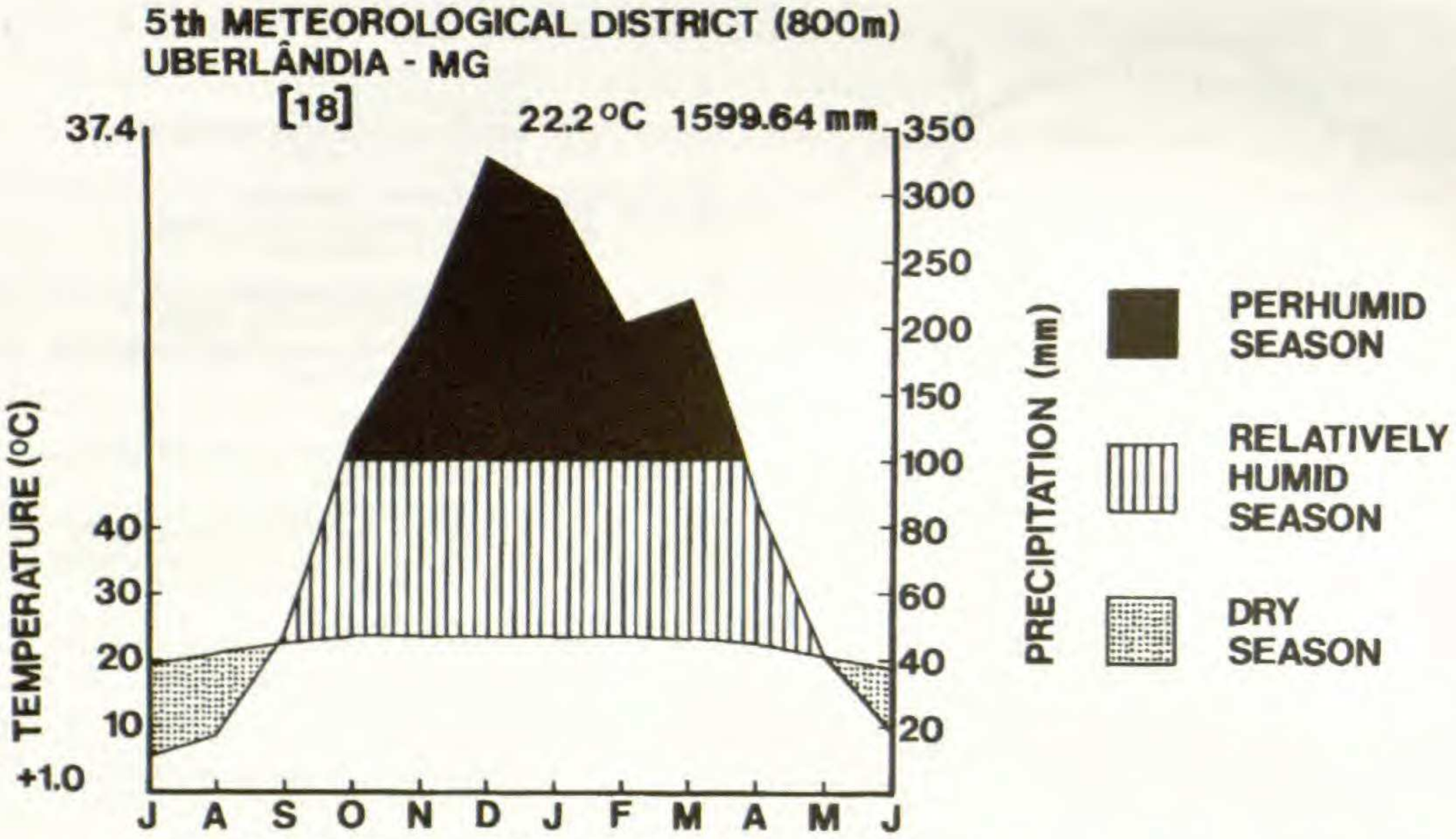

FIG. 2. Climate diagram of Uberlândia, Minas Gerais, Brazil for the period 1981–1998.

different depths was collected by introducing into each hole plastic tubes with a diameter of 2 cm, parallel to the soil surface. After collection, from the bottom to the top of the hole to prevent contamination, each portion of soil was stored in a plastic bag that was labelled and closed immediately. In the laboratory, soil was homogenized manually inside the bags, transferred to quadrangular, transparent, covered plastic boxes (experimental units), and moistened with distilled water. The superficial area of cultured soil was used to calculate the number of gametophytes and sporophytes formed per square centimeter. The number of gametophytes was the criterion used to evaluate viable spores in the soil samples. As indicated in Table 1, for the February 1997 and September 1998 collections, each portion of soil was divided in two sub-portions. Thus, 60 experimental units (boxes containing soil) could be examined daily for counting gametophytes and 60 experimental units were maintained intact for counting sporophytes at the end of the experiments.

Culture conditions are presented in Table 1. All cultures were periodically moistened with distilled water and, after two months of culture when gametophytes and young sporophytes presented the first signals of chlorosis, with nutrient solution (Meyer *et al.*, 1963) every 15 days. Sterilized soil controls (10 replicates) were maintained under the same laboratory conditions.

Forty days after each collection, when the gametophytes were at least 1 mm wide, the samples were examined daily under a stereomicroscope to count and remove gametophytes. Because gametophytes were removed at a relatively young age, it was possible to take them out without removing soil particles. The gametophytes removed from the soil were subsequently placed on a microscope slide and examined to search for additional germinating spores or gametophytes at the filamentous stage that might have been undetected under the stereomicroscope. The counting was concluded when the cultures were four months old.

Sporophytes were counted between three and four months after the initiation of the experiments, in intact soil of the duplicate cultures collected in February 1997 and September 1998. The criterion for counting sporophytes was the presence of a perceptible crozier when viewed under stereomicroscope. At the end of the experiments young sporophytes were transplanted to bags containing soil and were maintained under greenhouse conditions until the production of fertile leaves when they were collected. The collected sporophytes were prepared and deposited at HUFU and SP. Some specimens of *Thelypteris* were also deposited at UC and SI.

The experimental unit used to calculate the percentage of gametophytes forming sporophytes consisted of two duplicates. As was described above, for February 1997 and September 1998 collections, one duplicate of soil was used for counting gametophytes without replacement, and the other for counting sporophytes at the end of the experiments. Thus, the percentage was calculated as the proportion of sporophytes to gametophytes in the duplicates.

Systematic sampling was used to collect soil samples, due to the known differences among the three analysed microhabitats. The experimental units were randomly distributed in laboratory conditions. The number of gametophytes and sporophytes formed per square centimeter of cultured soil, as well as the percentage of gametophytes forming sporophytes, were submitted to the Shapiro-Wilk test. As part of the original and transformed data showed non-normality, the Mann-Whitney test was used for pairwise comparisons within microhabitats, depths, and collection dates.

Results

Gametophyte densities on cultured soil ranged from 0.13 to 29.52 gametophytes per square centimeter and, in general, 'dike' presented soil with lower mean numbers of viable spores than the other microhabitats (Table 2). The number of viable spores was higher at 2–4 and 5–7 cm depth than at 15–17 and 20–22 cm depth. The 'edge' of the forest showed fewer viable spores at 2–4 cm depth in April 1998 than in February 1997 collection, at the same depth (Tables 2, 3). Data from the April collection showed the existence of viable spores below 20–22 cm. All soil sample controls remained free of gametophytes during the experimental period, indicating no contamination of the cultures.

There is seasonality in the size of the soil spore bank of the gallery forest in the first centimeters of soil column as shown in Tables 2 and 3. Soil collected in February 1997, during the wet season, was richer in viable spores than soil collected in September 1997, at the end of the dry season. Soil samples collected at the end of dry season presented statistical differences between consecutive years only for the first centimeters of soil collected in the 'dike'. Soil collected in September 1997 presented lower number of viable spores than that collected in September 1998. As there was high variability among the replicates of the same sample, the statistical test used was not capable of detecting other differences (see the standard error of the means).

TABLE 1. Culture conditions to which soil samples collected in the gallery forest of the Panga Stream, Uberlândia, MG were submitted in order to quantify the soil spore bank.

Collection date	Microhabitat	Depth (cm)	Replication number	Area of cultured soil (cm^2)[1]	Temperature (°C)[2]	Light conditions ($\mu molm^{-2}\ s^{-1}$)[3]	Photoperiodic conditions	Evaluated characteristics
Feb 1997	D M E	2–4	5	11.67	23.36 ± 0.93	48.93	12	g
		5–7	5	11.67	23.36 ± 0.93	48.93	12	g
		15–17	5	11.67	23.36 ± 0.93	48.93	12	g
		20–22	5	11.67	23.36 ± 0.93	48.93	12	g
Feb 1997	D M E	2–4	5	11.67	23.36 ± 0.93	48.93	12	s
		5–7	5	11.67	23.36 ± 0.93	48.93	12	s
		15–17	5	11.67	23.36 ± 0.93	48.93	12	s
		20–22	5	11.67	23.36 ± 0.93	48.93	12	s
Sep 1997	D M E	2–4	10	10.73	23.51 ± 1.34	48.93	12	g
		5–7	10	10.73	23.51 ± 1.34	48.93	12	g
		15–17	10	10.73	23.51 ± 1.34	48.93	12	g
		20–22	10	10.73	23.51 ± 1.34	48.93	12	g
Apr 1998	E	2–4	20	11.07	23.28 ± 0.79	50.72	12	g
		30–32	20	11.07	23.28 ± 0.79	50.72	12	g
Sep 1998	D M E	2–4	5	10.42	23.18 ± 0.32	54.22	12	g
		5–7	5	10.42	23.18 ± 0.32	54.22	12	g
		15–17	5	10.42	23.18 ± 0.32	54.22	12	g
		20–22	5	10.42	23.18 ± 0.32	54.22	12	g
Sep 1998	D M E	2–4	5	10.42	21.79–22.84	43.45	c. l.	s
		5–7	5	10.42	21.79–22.84	43.45	c. l.	s
		15–17	5	10.42	21.79–22.84	43.45	c. l.	s
		20–22	5	10.42	21.79–22.84	43.45	c. l.	s

D M E: 'dike', 'middle', and 'edge' of the gallery forest; g: gametophyte; s: sporophyte; c.l.: continuous light; [1] mean; [2] minimum–maximum mean or mean ± standard deviation; [3] irradiance (PAR mean) was measured with a LI-COR LI-250 light meter and a LI-190SA quantum sensor.

TABLE 2. Gametophytes (mean ± standard error) produced in soil collected in the gallery forest of the Ecological Station of Panga, Uberlândia, MG.

Collection date	Depth (cm)	'Dike'		'Middle'		'Edge'	
		g cm^{-2}	*W*	g cm^{-2}	*W*	g cm^{-2}	*W*
Feb. 1997	2–4	4.03 ± 0.62 bA	**0.8995**	19.93 ± 5.06 aA	**0.915**	29.52 ± 4.27 aA	**0.9091**
	5–7	4.38 ± 1.00 bA	**0.8363**	12.06 ± 7.00 abA	0.6891	19.88 ± 4.72 aA	**0.8779**
	15–17	0.42 ± 0.21 bB	**0.8295**	1.14 ± 0.50 abB	**0.8932**	5.70 ± 2.24 aB	**0.9549**
	20–22	0.25 ± 0.14 bB	**0.8137**	0.51 ± 0.31 abB	**0.8099**	3.18 ± 1.57 aB	**0.8347**
Sep. 1997	2–4	1.36 ± 0.31 cA	**0.8848**	4.66 ± 0.67 bA	**0.9021**	9.26 ± 0.88 aA	**0.9094**
	5–7	0.96 ± 0.27 bAB	**0.8860**	3.12 ± 0.35 aA	0.7717	6.76 ± 1.56 aAB	**0.8992**
	15–17	0.37 ± 0.10 bB	0.8423	0.27 ± 0.09 bB	**0.9232**	4.20 ± 0.71 aB	**0.9718**
	20–22	0.14 ± 0.08 bC	0.6585	0.13 ± 0.05 bB	0.8346	1.37 ± 0.37 aC	**0.9377**
Apr. 1998	2–4	—	—	—	—	18.59 ± 2.15 A	**0.9333**
	30–32	—	—	—	—	0.73 ± 0.26 B	0.6039
Sep. 1998	2–4	4.32 ± 0.89 bA	**0.8993**	5.71 ± 1.42 bA	**0.8881**	14.01 ± 4.31 aA	0.7551
	5–7	3.97 ± 1.09 aAB	**0.7882**	3.23 ± 1.20 aA	**0.9151**	6.89 ± 1.62 aA	**0.9022**
	15–17	1.02 ± 0.43 bB	**0.8780**	0.28 ± 0.10 bB	**0.9970**	6.84 ± 2.28 aA	**0.8721**
	20–22	0.87 ± 0.66 abB	0.6805	0.13 ± 0.09 bB	0.7593	3.82 ± 2.17 aA	**0.8077**

g cm^{-2}: gametophytes per square centimeter of the cultured soil; *W*: Shapiro-Wilk test ($\alpha = 0.05$), where boldfaced values indicate normality of the studied characteristic in the population ($P > 0.05$); mean followed by the same lower case letter in each line and by the same capital letter in each column, within the same collection date, are not significantly different based on the Mann-Whitney test ($\alpha = 0.05$); —: without information.

The number of sporophytes formed on the cultured soil decreased with depth, as was observed also for the number of gametophytes formed (Table 4). Similar numbers of sporophytes were formed in the three microhabitats analyzed. The reproductive success of the viable spores encountered in the soil, calculated as the percentage of gametophytes forming sporophytes, ranged from 0.76% at 20–22 cm depth in soil of the 'edge' of the forest to 63.33% at the same depth in soil of the 'dike', both values registered for February 1997 collection (Table 5). Due to high variability among replicates of the same sample, few statistical differences in relation to depth and microhabitats were detected.

The sporophyte frequency per species for soil collected in September 1998 shows that *Thelypteris* species predominated in the three microhabitats and four depths (Table 6). This genus was better represented than the others, presenting nine species, while *Blechnum* presented two species and the other genus one species each (Table 7).

Sporophytes of 13 terrestrial species were registered in the analysed soil of the gallery forest of Panga Stream (Table 7). Five of these species were found from 2–4 to 30–32 cm depth, in the three microhabitats of the gallery forest (*Blechnum brasiliense* Desv., *Macrothelypteris torresiana* (Gaud.) Ching, *Pityrogramma calomelanos* (L.) Link var. *calomelanos*, *Thelypteris conspersa* (Schrad.) A. R. Sm., and *T. opposita* (Vahl) Ching). The September 1998 collection provided more complete information about species composition of the soil spore bank due to the high survival rate of the sporophytes after

TABLE 3. Multiple comparisons for gametophytes formed in soil samples collected in the gallery forest, Ecological Station of Panga, Uberlândia, MG. The mean values and the dispersion measurements are included in Table 2.

Collection date	Depth (cm)	'Dike'		'Middle'		'Edge'	
		U value	P value	*U* value	P value	*U* value	P value
Feb × Sep 1997	2–4	48	0.0027	49	0.0013	50	0.0007
	5–7	48	0.0027	40	0.0753	43	0.0280
	15–17	18	0.3100	40	0.0753	28	0.7680
	20–22	28	0.7680	33	0.3710	33	0.3710
Feb 1997 × Apr 1998	2–4	—	—	—	—	81	0.0351
Sep 1997 × 1998	2–4	45	0.0127	30	0.5940	31	0.5130
	5–7	47	0.0047	26	0.9530	26.5	0.8590
	15–17	39	0.0992	26.5	0.8590	31	0.5130
	20–22	36	0.2060	27.5	0.7680	29	0.6790

P: probability to accept or reject the null hypothesis; $P > 0.05$ means that the two medians are not significantly different; $P < 0.05$ means that the two medians are significantly different; *U*: statistic of the Mann-Whitney test.

transplanting. Considering the four collection dates, a similar number of species was observed in the three microhabitats of the forest. The number of species decreased with depth (Table 7, September 1998).

DISCUSSION

The range of viable spores included in soil samples of the gallery forest of Panga Stream was similar to that reported by Dyer and Lindsay (1992) for soil samples collected in Durham, N.C., U.S.A. 'Dike' samples presented smaller numbers of viable spores when compared to the other microhabitats, perhaps as a consequence of the seasonal leaching of this microhabitat. Depending on the rainfall, there is a fast overflow of the stream, washing the litter deposited in the 'dike' toward the 'middle'. Alluvial deposition, consisting mainly of sand, occurs at the same time. Water reflux towards the streambed occurs rapidly, cleaning the sandy soil of the 'dike'. Movement of spores down through the soil probably occurs as the result of the percolation of rain water, rather than by inundation.

Preliminary data about the distribution of adult sporophytes in the studied area (personal observation), evaluated using one transect of 190 m^2 per microhabitat, with observations in 10 quadrats of 1 m^2 per transect, indicated no significant differences between the three microhabitats ($W = 0.607$, $P = 0.7381$ for Kruskal-Wallis test). 'Dike' presented 0.9 ± 1.45, 'middle' 0.5 ± 0.97, and 'edge' 0.3 ± 0.48 sporophytes per square meter (mean $\pm$ standard deviation). These results indicate that the differences between microhabitats in soil spore bank densities are not a consequence of differential adult sporophyte distribution in the studied area.

A decrease in the number of viable spores with increasing depth was also registered by Leck and Simpson (1987) for high marsh, cattail, and shrub forest in a Delaware River freshwater tidal wetland, by Lindsay and Dyer (1990) for

TABLE 4. Sporophytes (mean ± standard error) produced in soil collected in the gallery forest of the Ecological Station of Panga, Uberlândia, MG.

Collection date	Depth (cm)	'Dike'		'Middle'		'Edge'	
		s cm^{-2}	*W*	s cm^{-2}	*W*	s cm^{-2}	*W*
Feb. 1997	2–4	1.49 ± 0.24 bA	**0.9348**	4.30 ± 1.45 aA	**0.8216**	5.75 ± 0.89 aA	**0.8940**
	5–7	0.73 ± 0.35 aAB	**0.8478**	1.32 ± 0.72 aAB	**0.7928**	4.09 ± 1.57 aA	**0.9287**
	15–17	0.22 ± 0.13 aB	**0.8327**	0.16 ± 0.10 aB	0.7426	0.84 ± 0.60 aB	0.6965
	20–22	0.27 ± 0.17 aB	0.7476	0.26 ± 0.18 aB	0.7708	0.05 ± 0.03 aB	0.7675
Sep. 1998	2–4	1.21 ± 0.46 aA	**0.8387**	2.29 ± 0.54 aA	**0.8935**	3.77 ± 1.26 aA	**0.9465**
	5–7	0.92 ± 0.64 aAB	0.6684	1.32 ± 0.42 aA	**0.9017**	1.67 ± 0.44 aAB	**0.8179**
	15–17	0.18 ± 0.11 aB	0.7425	0.06 ± 0.04 aB	0.7679	0.44 ± 0.18 aB	**0.9642**
	20–22	0.28 ± 0.28 aAB	0.5521	0.09 ± 0.06 aB	0.7612	0.39 ± 0.30 aB	0.6884

s cm^{-2}: sporophytes per square centimeter of the cultured soil; *W*: Shapiro-Wilk test ($\alpha = 0.05$), where boldfaced values indicate normality of the studied characteristic in the population ($P > 0.05$); mean followed by the same lower case letter in each line and by the same capital letter in each column, within the same collection date, are not significantly different based on the Mann-Whitney test ($\alpha = 0.05$).

forests near Edinburgh, Scotland, by Dyer and Lindsay (1992) for several places in North Carolina and Scotland, and by Simabukuro *et al.* (1998, 1999) for areas of cerrado in São Paulo, Brazil. This pattern is also similar to that observed in soil seed banks of forest, savanna, and farmlands of tropical regions (Garwood, 1989). According to Fenner (1995), all studies of vertical distribution of seeds in soil indicate that in undisturbed sites the vast majority of seeds are found in the first 2–5 cm of soil, with a notable decline in numbers with depth.

Gametophytes and sporophytes developed more slowly on soil collected in the gallery forest of Panga Stream from 15–17 to 30–32 cm depth than in the more superficial layers, although periodically moistened with nutrient solution. Moreover, some sporophytes had anomalous morphology although transplanted to good soil after their formation. These observations indicate that some of the spores located at greater depths, and which germinated under laboratory conditions, could be older than spores included in soil collected from the first centimeters. Anomalies and slow gametophyte development observed for some species when old spores were used for culture in laboratory conditions (Raghavan, 1980) reinforce this idea.

Probably the decrease of viable spores observed at the end of the dry season, especially in the first centimeters of the soil, is in part a consequence of death by desiccation. On the other hand, the decrease in the size of the soil spore bank registered in April in relation to February shows that some spores can germinate from February to April when rainfall decreases gradually, but the soil has sufficient water accumulated during the wet season.

Although phenology of the fern species of Ecological Station of Panga is unknown, periodic observations indicate that for some species production of new leaves occurs in October–November, at the beginning of the rainy season, and the production of fertile leaves occurs in December–January. Seasonality of

TABLE 5. Percentage of gametophytes forming sporophytes (mean ± standard error) calculated for soil collected in the gallery forest of Ecological Station of Panga, Uberlândia, MG.

Collection date	Depth (cm)	'Dike' % g	'Dike' *W*	'Middle' % g	'Middle' *W*	'Edge' % g	'Edge' *W*
Feb. 1997	2–4	43.72 ± 11.98 aA	**0.9455**	20.77 ± 2.50 aA	**0.8940**	20.01 ± 2.18 aA	**0.8518**
	5–7	27.01 ± 18.51 aA	0.7094	10.75 ± 1.99 aB	**0.9434**	17.81 ± 4.89 aA	**0.8863**
	15–17	42.67 ± 20.50 aA	**0.8747**	16.98 ± 11.39 aAB	0.7694	26.85 ± 18.83 aAB	0.7365
	20–22	63.33 ± 22.61 aA	0.7331	30.53 ± 20.14 aAB	0.7726	0.76 ± 0.47 aB	0.6888
Sep. 1998	2–4	26.00 ± 8.83 aA	**0.8945**	44.17 ± 6.22 aA	**0.9479**	25.67 ± 9.16 aA	**0.9077**
	5–7	16.49 ± 8.12 abA	0.6856	45.93 ± 3.95 aA	**0.9895**	20.90 ± 5.89 bA	**0.9273**
	15–17	9.56 ± 6.04 aA	0.7657	13.33 ± 8.16 aB	0.6839	9.99 ± 6.02 aA	**0.8105**
	20–22	8.00 ± 8.00 aA	0.5521	32.00 ± 20.59 aAB	0.7725	5.97 ± 2.95 aA	**0.8747**

% g: percentage of gametophytes forming sporophytes on surface of the cultured soil; *W*: Shapiro-Wilk test ($\alpha = 0.05$), where boldfaced values indicate normality of the studied characteristic in the population ($P > 0.05$); mean followed by the same lower case letter in each line and by the same capital letter in each column, within the same collection date, are not significantly different based on the Mann-Whitney test ($\alpha = 0.05$).

fertile leaves was also observed for some species occurring in a mesophytic, semideciduous forest in the State of São Paulo, under similar rain distribution conditions (Ranal, 1995). In the gallery forest of Panga, spore dispersal occurs from December (precocious leaves) to March–April (late leaves), depending on the annual rainfall distribution. Thus, the seasonality of the soil spore bank observed for this gallery forest, especially in the first centimeters of soil column, may be a consequence of the seasonality in spore production and of the gradual loss of viability associated with desiccation of the soil that occurs during the dry season. Seasonality in soil spore banks was also registered in a flooded mountain meadow in Patagonia, Argentina (Raffaele, 1996). The soil spore bank of *Dennstaedtia punctilobula* (Michx.) Moore varied across pre- and post-dispersal seasons in two undisturbed hardwood forest sites in central Pennsylvania (Penrod and McCormick, 1996).

According to Garwood (1989), unpredictable rainfall during the dry season also causes seed death in tropical regions. The distribution of rainfall registered in the region of Uberlândia in 1997 was atypical in relation to former years. In April 149.8 mm of precipitation was registered, while the mean of the previous 18 years was 87.0 mm; in June 105.1 mm was registered while the mean for the same 18-year period was 19.0 mm. Certainly abundant water in the soil, stimulating precocious germination, followed by low precipitation (36.3 mm in May and zero in July and August), was an important cause of the decrease of viable spores in the soil observed in September 1997 in relation to September 1998 for 'dike' of the forest. Moreover, the precipitation registered in 1997 (1811 mm) was higher than the mean of the previous 18 years (1599.64 mm). As a consequence the level of the stream increased, washing the 'dike' more than in 1998. In 1998 the precipitation was 1356.7 mm. Evidences for variation in size or species composition of the seed bank from one year to another is scanty (Garwood, 1989).

TABLE 6. Sporophyte frequency (mean percentage) registered in soil collected in September 1998, in the gallery forest of the Ecological Station of Panga. Values were calculated in relation to the total number of sporophytes formed in the replicates. Data obtained three months after the collection of soil.

Depth (cm)	Species	'Dike'	'Middle'	'Edge'
2–4	*Thelypteris* spp.	71.03	88.31	100.00
	Pityrogramma calomelanos (L.) Link var. *calomelanos*	4.30	2.31	0.00
	Lygodium venustum Sw.	4.00	0.00	0.00
	Blechnum brasiliense Desv.	0.67	9.37	0.00
5–7	*Thelypteris* spp.	76.57	88.81	98.68
	Pityrogramma calomelanos (L.) Link var. *calomelanos*	3.43	10.36	0.00
	Lygodium venustum Sw.	0.00	0.00	0.00
	Blechnum brasiliense Desv.	0.00	0.83	1.32
15–17	*Thelypteris* spp.	50.00	75.00	100.00
	Pityrogramma calomelanos (L.) Link var. *calomelanos*	12.50	0.00	0.00
	Lygodium venustum Sw.	12.50	0.00	0.00
	Blechnum brasiliense Desv.	0.00	25.00	0.00
20–22	*Thelypteris* spp.	100.00	100.00	100.00
	Pityrogramma calomelanos (L.) Link var. *calomelanos*	0.00	0.00	0.00
	Lygodium venustum Sw.	0.00	0.00	0.00
	Blechnum brasiliense Desv.	0.00	0.00	0.00

Although high numbers of viable spores were registered in soil collected in February 1997 at 2–4 cm depth in the 'middle' and in the 'edge' of the forest, only 20% of gametophytes produced sporophytes. These results, obtained in protected laboratory conditions, without biotic and abiotic disturbances, show the importance of the high number of spores produced by sporophytes for fern establishment. It means that the efficacy of viable spores for fern establishment and the role of the soil spore bank in the dynamics of the plant communities can be better inferred by looking at sporophytes formed. The efficacy of soil seed banks can be evaluated directly simply by counting seedlings formed, but in ferns, the gametophytic phase with its peculiar ecophysiological and reproductive characteristics can lead to different results.

The 13 species found as viable spores in soil samples of the gallery forest represent about 25% of the 52 fern species currently registered for the Ecological Station of Panga (Prado and Ranal, unpublished data). These species represent an addition to the list of species capable of forming soil spore banks presented by Dyer and Lindsay (1992). The soil seed bank of this gallery forest, evaluated in 1998 and 1999, also presented lower diversity than the actual vegetation, with 17% of species present as viable seeds (Pereira, 1999). According to Fenner (1985), in frequently disturbed habitats the species composition of the seed bank and the vegetation are usually similar, but as the vegetation matures the disparity between the two increases, and in general seed banks have lower diversity than the aboveground vegetation. Several

TABLE 7. Species that are able to form soil spore bank in the gallery forest of the Ecological Station of Panga, Uberlândia, MG.

Collection Date	Depth (cm)	'Dike'	NS	'Middle'	NS	'Edge'	NS	Total
Feb 1997	2–4	—	—	*Pityrogramma calomelanos* (L.) Link var. *calomelanos*	1	—	—	**1**
	5–7	—	—	*Pityrogramma calomelanos* (L.) Link var. *calomelanos*	1	—	—	
	15–17	—	—	*Pityrogramma calomelanos* (L.) Link var. *calomelanos*	1	—	—	
	20–22	—	—	—	—	*Pityrogramma calomelanos* (L.) Link var. *calomelanos*	1	
Sep 1997	2–4	*Lygodium venustum* Sw. *Pityrogramma calomelanos* (L.) Link var. *calomelanos* *Thelypteris opposita* (Vahl) Ching	3	*Blechnum brasiliense* Desv. *Lygodium venustum* Sw. *Pityrogramma calomelanos* (L.) Link var. *calomelanos* *Thelypteris hispidula* (Decne) C. F. Reed	4	—	—	**5**
	5–7	*Lygodium venustum* Sw.	1	*Pityrogramma calomelanos* (L.) Link var. *calomelanos* *Thelypteris hispidula* (Decne) C. F. Reed *Thelypteris interrupta* (Willd.) Iwats. *Thelypteris opposita* (Vahl) Ching	4	*Pityrogramma calomelanos* (L.) Link var. *calomelanos*	1	**5**
	15–17	*Lygodium venustum* Sw.	1	*Macrothelypteris torresiana* (Gaud.) Ching *Pityrogramma calomelanos* (L.) Link var. *calomelanos* *Thelypteris opposita* (Vahl) Ching	3	—	—	**4**
	20–22	*Lygodium venustum* Sw.	1	*Pityrogramma calomelanos* (L.) Link var. *calomelanos*	1	—	—	**2**

TABLE 7. Continued.

Collection Date	Depth (cm)	'Dike'	NS	'Middle'	NS	'Edge'	NS	Total
Apr 1998	30–32	—	—	—	—	*Blechnum brasiliense* Desv. *Macrothelypteris torresiana* (Gaud.) Ching *Pityrogramma calomelanos* (L.) Link var. *calomelanos* *Thelypteris conspersa* (Schrad.) A. R. Sm. *Thelypteris opposita* (Vahl) Ching *Thelypteris* sp.	6	**6**
Sep 1998	2–4	*Blechnum brasiliense* Desv. *Blechnum occidentale* L. *Lygodium venustum* Sw. *Pityrogramma calomelanos* (L.) Link var. *calomelanos* *Thelypteris dentata* (Forssk.) E. St. John *Thelypteris hispidula* (Decne) C. F. Reed *Thelypteris mosenii* (C. Chr.) C.F. Reed *Thelypteris opposita* (Vahl) Ching	8	*Blechnum brasiliense* Desv. *Macrothelypteris torresiana* (Gaud.) Ching *Pityrogramma calomelanos* (L.) Link var. *calomelanos* *Thelypteris conspersa* (Schrad.) A. R. Sm. *Thelypteris dentata* (Forssk.) E. St. John *Thelypteris hispidula* (Decne) C. F. Reed *Thelypteris interrupta* (Willd.) Iwats. *Thelypteris opposita* (Vahl) Ching	8	*Blechnum brasiliense* Desv. *Macrothelypteris torresiana* (Gaud.) Ching *Thelypteris conspersa* (Schrad.) A. R. Sm. *Thelypteris dentata* (Forssk.) E. St. John *Thelypteris hispidula* (Decne) C. F. Reed *Thelypteris opposita* (Vahl) Ching *Thelypteris patens* (Sw.) Small	7	**12**
	5–7	*Lygodium venustum* Sw. *Pityrogramma calomelanos* (L.) Link var. *calomelanos* *Thelypteris opposita* (Vahl) Ching	3	*Blechnum brasiliense* Desv. *Macrothelypteris torresiana* (Gaud.) Ching *Pityrogramma calomelanos* (L.) Link var. *calomelanos*	6	*Blechnum brasiliense* Desv. *Macrothelypteris torresiana* (Gaud.) Ching *Pityrogramma calomelanos* (L.) Link var. *calomelanos*	6	**8**

TABLE 7. Continued.

Collection Date	Depth (cm)	'Dike'	NS	'Middle'	NS	'Edge'	NS	Total
	5–7 cont.			*Thelypteris dentata* (Forssk.) E. St. John *Thelypteris hispidula* (Decne) C. F. Reed *Thelypteris opposita* (Vahl) Ching		*Thelypteris conspersa* (Schrad.) A. R. Sm. *Thelypteris hispidula* (Decne) C. F. Reed *Thelypteris opposita* (Vahl) Ching		
	15–17	*Lygodium venustum* Sw. *Pityrogramma calomelanos* (L.) Link var. *calomelanos*	2	*Blechnum brasiliense* Desv. *Thelypteris interrupta* (Willd.) Iwats.	2	*Thelypteris conspersa* (Schrad.) A. R. Sm. *Thelypteris opposita* (Vahl) Ching	2	**6**
	20–22	*Macrothelypteris torresiana* (Gaud.) Ching *Thelypteris conspersa* (Schrad.) A. R. Sm. *Thelypteris dentata* (Forssk.) E. St. John *Thelypteris opposita* (Vahl) Ching	4	*Thelypteris opposita* (Vahl) Ching	1	*Thelypteris conspersa* (Schrad.) A. R. Sm.	1	**4**
Total			**10**		**9**		9	**13**

NS: number of species.

studies of angiosperm population dynamics in the gallery forest of Panga Stream indicated that the seedling bank, with high diversity, is an efficient form of regeneration in this forest (Oliveira and Schiavini, 1999). There is no information about fern population dynamics, but these results indicate that this forest could support only short-term disturbances and needs to be preserved. This kind of information is important to give support to conservation projects for gallery forests that are endangered, although protected by law.

Decrease in the number of fern species occurring in the soil column was similar to the observations made for soil seed banks in several soil profiles in forest, savanna, and farmlands, according to a review presented by Garwood (1989) for tropical regions. In agricultural environments, due to the soil movement in relatively short periods, the vertical distribution of spores can be different, as was observed for seeds by Cavers and Benoit (1989).

Although studies of soil spore banks are recent in relation to soil seed banks, a comparison of different results is difficult due to diverse methods of collection of soil and counting of viable spores. There is information concerning the frequency of viable spores per hectare (Wee, 1974), per square meter (Milberg, 1991), per square centimeter (Dyer and Lindsay, 1992) and viable spores per volume of soil (Hamilton, 1988). The numbers are mentioned in relation to gametophyte formation (Lindsay and Dyer, 1990; Milberg, 1991; Dyer and Lindsay, 1992; Milberg and Anderson, 1994), but according to Milberg (1991) some authors perhaps had counted the number of sporophytes formed and some of them did not specify their adopted criterion. Considering that one species can produce some exclusively male gametophytes and some exclusively female, which remain unfertilized due to incompatibility or other problems, it would seem more accurate to estimate viable spores by the number of gametophytes formed.

High variability in the numbers of gametophytes formed in the soil collected in the gallery forest of Panga Stream shows that deposition of spores in the soil is heterogeneous. A similar condition exists for soil seed banks (Garwood, 1989; Baskin and Baskin, 1998). According to Fenner (1995) the heterogeneity of the horizontal distribution of the seeds, resulting in a high degree of variability between samples, is one of the main problems in obtaining good quantitative data on seed banks. Thus, it seems more appropriate to express the results as gametophytes per square centimeter in relation to cultured soil, without greater extrapolations. The counting of viable spores by means of number of gametophytes formed on the cultured soil is itself a relative measurement. Certainly some of the spores in the samples remains dormant due to the artificial culture conditions that vary between laboratories. This high variability among soil samples due to the heterogeneous horizontal distribution of the dispersion units makes it difficult to detect differences between microhabitats, depths or other factors.

Another important point is the timing of observations. During the experimental period of this study, gametophytes were removed from the soil as soon as they reached 1–2 mm. In this manner, few of them died before counting. Soil used to count sporophytes that were maintained intact during

three or four months showed several gametophytes in necrosis at the end of the experiment. Certainly, if the counting took place only at the end of the experiments, the number of gametophytes per square centimeter would be different because several gametophytes would be completely decomposed. Moreover, at three or four months of age, several gametophytes presented vegetative growth that made counting difficult because they formed wrinkled and crowded blades. Part of this vegetative growth was observed as young gametophytes formed in the mother tissue. These gametophytes could be separated and counted inadequately as resulting from spore germination when, in fact, they are vegetative growths of the mother gametophyte. On the other hand, the few rhizoids of young gametophytes removed from the cultured soil, method adopted in this study, can drag spores to the soil surface giving rise to an overvaluation of the soil spore bank. These technical problems pointed out mean that all methods used until now can not evaluate the absolute number of viable spores in the soil, but can be used only as an estimate.

The literature accumulated during these years permits the conclusion that the soil seed bank can consist of a mixture of transient and persistent species (Fenner, 1995). A species is considered to be transient in the seed bank if its seeds do not persist in the soil in a viable condition for more than a year. These seeds depend on regeneration opportunities such as seasonal gap formation to start the germination process. The persistent seed banks usually characterize plant communities that are submitted to frequent and unpredictable disturbances where opportunities for colonization occur at random and the seeds must remain viable in the soil more than one year. Certainly there are intermediate species between these two described types (Fenner, 1995). These ideas were also presented by Thompson and Grime (1979), Simpson *et al.* (1989), and Bewley and Black (1994). Although there is less information about fern spore banks, analogous characteristics of germination physiology in seeds and fern spores permits the inference that these two types of species can also be found among the ferns. The principal difficulty in establishing these categories for fern species is the insufficient knowledge on the phenology of spore production, the longevity of spores for the majority of species, and the dynamics of the spore movement process through the soil column.

A new and dynamic approach, more related to environmental questions, was given by Walck *et al.* (1996) and adopted by Baskin and Baskin (1998). The authors suggested that these two types of seed banks should be described in terms of germination seasons rather than age *per se.* Thus, a transient seed bank is composed of seeds that do not live beyond the first germination season following maturation, and a persistent seed bank is composed of seeds that can live until the second germination season or more than this (Baskin and Baskin, 1998). In this sense, data obtained at the end of the dry season for the gallery forest of Panga Stream could give an idea about the size of the persistent soil spore bank of that environment. The low pluviosity characteristic of the dry winter in the region causes a slower plant growth rate and new spore production will occur only in the next wet season. Thus, there is no new

significant addition to the spore stock from April to September and the germination season will occur in October–November, when rainfall starts.

As the gallery forest of the Panga Stream presented higher numbers of viable spores and higher numbers of species in the first centimeters of soil column than in deep soil, it appears that this ecosystem is in good conservation status. Nevertheless, its lower diversity than the actual vegetation, typical of preserved environments, indicates that this forest must be protected against anthropic actions.

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